

Egg sizes of nine passerine bird species in a subalpine birch forest, Swedish Lapland

ANDERS ENEMAR & OLA ARHEIMER

Abstract

Egg measurements together with calculated volumes are presented for nine passerine species (*Prunella modularis*, *Luscinia svecica*, *Phoenicurus phoenicurus*, *Turdus pilaris*, *Turdus philomelos*, *Turdus iliacus*, *Phylloscopus trochilus*, *Fringilla montifringilla*, and *Carduelis flammea*), breeding in rich subalpine birch forests on a south-faced mountain slope in southern Swedish Lapland. There were no clear regional size trends in comparisons with egg collections from other parts of Europe. There was a significant increase in egg size in the latter part of the laying sequence. The ultimate egg is from 2.1% (*F. montifringilla*-

la) to 6.5% (*P. trochilus*) larger than the mean of the clutch. According to several years' measurements of *T. pilaris* and *T. iliacus* eggs there was no significant size variation between seasons. This constancy together with the relatively large egg sizes might be a consequence of the productive breeding habitat of the study area.

Anders Enemar, Zoological Institute, Box 463, S-405 30 Göteborg, Sweden.

Ola Arheimer, Magasinsvägen 58, S-681 53 Kristinehamn, Sweden.

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Introduction

Information on egg sizes in birds started to accumulate when egg collections were established by museums and private collectors. Egg collections may serve as an important source of information for descriptions in handbooks and for analyses of various scientific problems (e.g. Svensson 1978). During the last few decades egg sizes have been used in investigations of problems related to breeding biology. The egg size has then proved to be important, showing a considerable inter- as well as intraclutch variation. This variation may depend on the quality of the egg-laying female and a number of environmental factors. The latter create problems when data from different populations and regions are compared and analysed. Frequently information about the number of clutches, the frequency of repeat or secondary clutches, the time of the season, and so on, is faulty or lacking. Regional trends in clutch size were discovered long ago (cf. Lack 1968), but the corresponding knowledge regarding egg dimensions is still scanty. Some relevant data will be referred to in the following.

This report presents egg size and egg size variation of nine passerine bird species inhabiting subalpine birch forest in Swedish Lapland. The measurements were successively obtained in the LUVRE project, a long-term project primarily aimed at other problems than those related to egg size variation.

Study area and methods

The investigated bird populations breed in the southern part of Swedish Lapland on the south-facing slopes of the mountains of Gaisatjåkke and Valle. The habitat is mountain birch forests, mostly of a rich type "meadow birch forest". Locally this may turn into a less rich heath vegetation, especially in the upper parts. The area of the field work extends from the stream of Raurejukke in the west to the stream of Karsbäcken in the east. It is bordered in the south by the Lake Stor-Tjulträsket and the river Tjulån. The position of the area is approximately 65° 58'–65° 59' N, 15° 58'–16° 8' E, with an altitude of 540 to 720 m a.s.l. A small village, Ammarnäs, borders on the south-eastern corner of the area. We

Table 1. Egg measurements (mm), mean \pm SD. First line of each species = mean of all single eggs; second line = mean of clutch means.

Äggmått i mm, medelvärden \pm SD. Första raden för varje art = medelvärde för de enskilda äggen; andra raden = medelvärde för kullarnas medelvärden.

Species <i>Art</i>	n	Length <i>Längd</i>	C.V.	Range <i>Spridning</i>	Breadth <i>Bredd</i>	C.V.	Range <i>Spridning</i>
<i>Prunella modularis</i>	39	20.2 \pm 1.09	5.4	18.2–22.3	15.0 \pm 0.46	3.1	14.0–15.6
	8	20.2 \pm 1.11	5.5		15.0 \pm 0.47	3.1	
<i>Luscinia svecica</i>	50	19.5 \pm 0.74	3.8	17.8–20.6	14.5 \pm 0.26	1.8	13.8–15.0
	9	19.5 \pm 0.69	3.6		14.5 \pm 0.21	1.4	
<i>Phoenicurus phoenicurus</i>	66	18.7 \pm 0.90	4.8	16.4–20.8	14.1 \pm 0.36	2.6	13.4–14.8
	10	18.7 \pm 0.88	4.6		14.1 \pm 0.32	2.3	
<i>Turdus pilaris</i>	232	29.8 \pm 0.97	3.3	25.3–33.8	21.2 \pm 0.66	3.1	19.4–22.8
	90	29.8 \pm 1.10	3.7		21.2 \pm 0.63	3.0	
<i>Turdus philomelos</i>	120	28.5 \pm 1.45	5.1	23.1–31.4	20.8 \pm 0.75	3.6	18.5–23.0
	23	28.5 \pm 1.27	4.5		20.8 \pm 0.73	3.5	
<i>Turdus iliacus</i>	899	26.4 \pm 1.24	4.7	21.9–30.4	19.2 \pm 0.57	3.0	17.0–20.8
	157	26.4 \pm 1.07	4.0		19.2 \pm 0.66	3.4	
<i>Phylloscopus trochilus</i>	63	16.0 \pm 0.59	3.7	15.0–17.8	12.3 \pm 0.44	3.6	11.5–13.1
	11	16.0 \pm 0.55	3.4		12.3 \pm 0.41	3.4	
<i>Fringilla montifringilla</i>	87	20.1 \pm 0.88	4.4	17.6–22.0	14.8 \pm 0.65	4.4	13.4–16.4
	14	20.1 \pm 0.80	4.0		14.8 \pm 0.61	4.1	
<i>Carduelis flammea</i>	50	16.6 \pm 0.97	5.8	14.7–18.4	12.5 \pm 0.44	3.5	11.5–13.4
	10	16.6 \pm 0.76	4.6		12.5 \pm 0.39	3.2	

often use this name in the following when referring to the study area.

We measured eggs either directly in the field, as for most thrush clutches, or on slightly enlarged photographs of transilluminated clutches of the smaller species (Enemar & Arheimer 1989). We used sliding callipers that allowed readings to the nearest 0.1 or 0.05 mm. The enlarged measurements were scaled down using a correction factor from eggs that had been measured both in the field and on photographs (Enemar 1997). We calculated volumes according to Hoyt (1979). In order to establish the laying order we inspected a number of clutches each day and marked new eggs. We measured thrush eggs in 1971–1974, 1997, and 1998; and photographed the clutches of the remaining species in 1981–1985, 1989, 1990, and 1992. The statistical tests we use are

all parametric and two-tailed: two-sample t-tests, ANOVA, and regression (Bonnier & Tedin 1940).

Results

The lengths and breadths of the eggs are presented in Table 1 as the mean of all eggs and the mean of the clutch means. The former is normally used in older investigations and often cited in handbooks. With few exceptions, useful information on dispersion from the mean, like standard deviation, is lacking. The maximum and minimum values (range) are given instead, and to facilitate comparisons we therefore included also ranges in Table 1. However, statistical testing requires that samples are independent, meaning that only means of clutches can be used in comparisons. The two kinds of mean hardly

Table 2. Calculated egg volumes, cm³, mean ± SD of clutch means. n = number of clutches.

Beräknade äggvolymer, medelvärde av kullarnas medelvärden. n = antal kollar.

Species Art	n	Mean volume Medelvolym
<i>Prunella modularis</i>	8	2.32±0.242
<i>Luscinia svecica</i>	9	2.08±0.107
<i>Phoenicurus phoenicurus</i>	10	1.88±0.151
<i>Turdus pilaris</i>	90	6.87±0.566
<i>Turdus philomelos</i>	23	6.31±0.604
<i>Turdus iliacus</i>	157	4.97±0.356
<i>Phylloscopus trochilus</i>	11	1.24±0.081
<i>Fringilla montifringilla</i>	14	2.28±0.263
<i>Carduelis flammea</i>	10	1.32±0.109

differed in our samples (Table 1). On the other hand, the standard deviations of the single egg means exceeded those of the clutch means in 15 out of 18 comparisons. The calculated egg volumes are shown in Table 2.

The egg size variation in relation to the position of the egg in the laying sequence was investigated in the clutches with marked eggs. The result is shown in Figure 1 which shows percentage deviation from

the clutch means. The number of eggs compared in each position in the laying order may differ because some clutches were not followed from the first egg and some clutches were not visited every day. The sequence-dependent variation in the egg size was tested with parametric regression analysis.

The parameters of the regression lines are presented in Table 3. Egg size in general increases from the first to the last laid egg. The mean relative sizes of the last laid eggs are shown in Table 4.

Comparisons

The information on egg sizes from other populations and regions varies in quality, and the comparisons may not permit detailed analyses and firm conclusions. The data from populations outside Swedish Lapland are primarily from the reviews in the *Handbuch der Vögel Mitteleuropas* (Glutz von Blotzheim & Bauer 1985–1997). Other handbooks have also been used (Rosenius 1926–1929, Witherby et al. 1948, Haftorn 1971, Cramp 1988, 1992, Cramp & Perrins 1994). In addition we used the following oological handbooks: Rey (1912), Verheyen (1967), Makatsch (1976), and Schönwetter (1979, 1984). There are few investigations on the variation of egg sizes dealing with the species in this study.

Table 3. The slope (b) and regression coefficients (r) of the regression lines of egg size, expressed as percentage of clutch mean, upon position in the laying sequence. N = clutch size, n = number of eggs.

Prövning av sambandet mellan äggets storlek, uttryckt i procent av medelvärdet för kullen, och äggets plats i värvföljden. b = medelökningen av procenttalet från ägg till ägg i värvordningen, r = ett mått på styrkan i sambandet, p = maximala sannolikheten för att slumpen kan ha orsakat storleksökningen i värvföljden (n.s. = icke signifikant). N = kullstorlek, n = antal ägg.

Species	Art	N	n	r	B	p<
<i>Prunella modularis</i>		5	25	0.66	1.75	0.001
<i>Luscinia svecica</i>		5	25	0.60	1.66	0.01
		6	54	0.25	0.47	n.s.
<i>Phoenicurus phoenicurus</i>		6	25	0.43	1.06	0.05
		7	80	0.29	0.50	0.01
<i>Turdus pilaris</i>		6	74	0.74	2.05	0.001
		5	67	0.46	1.61	0.001
<i>Turdus iliacus</i>		5	26	0.76	2.75	0.001
		6	31	0.57	2.63	0.001
<i>Phylloscopus trochilus</i>		6	42	0.39	1.59	0.001
		7	30	0.57	1.54	0.01
<i>Fringilla montifringilla</i>		5	10	0.75	1.50	0.02
		6	35	0.44	0.79	0.01
<i>Carduelis flammea</i>		7	44	0.61	2.09	0.001

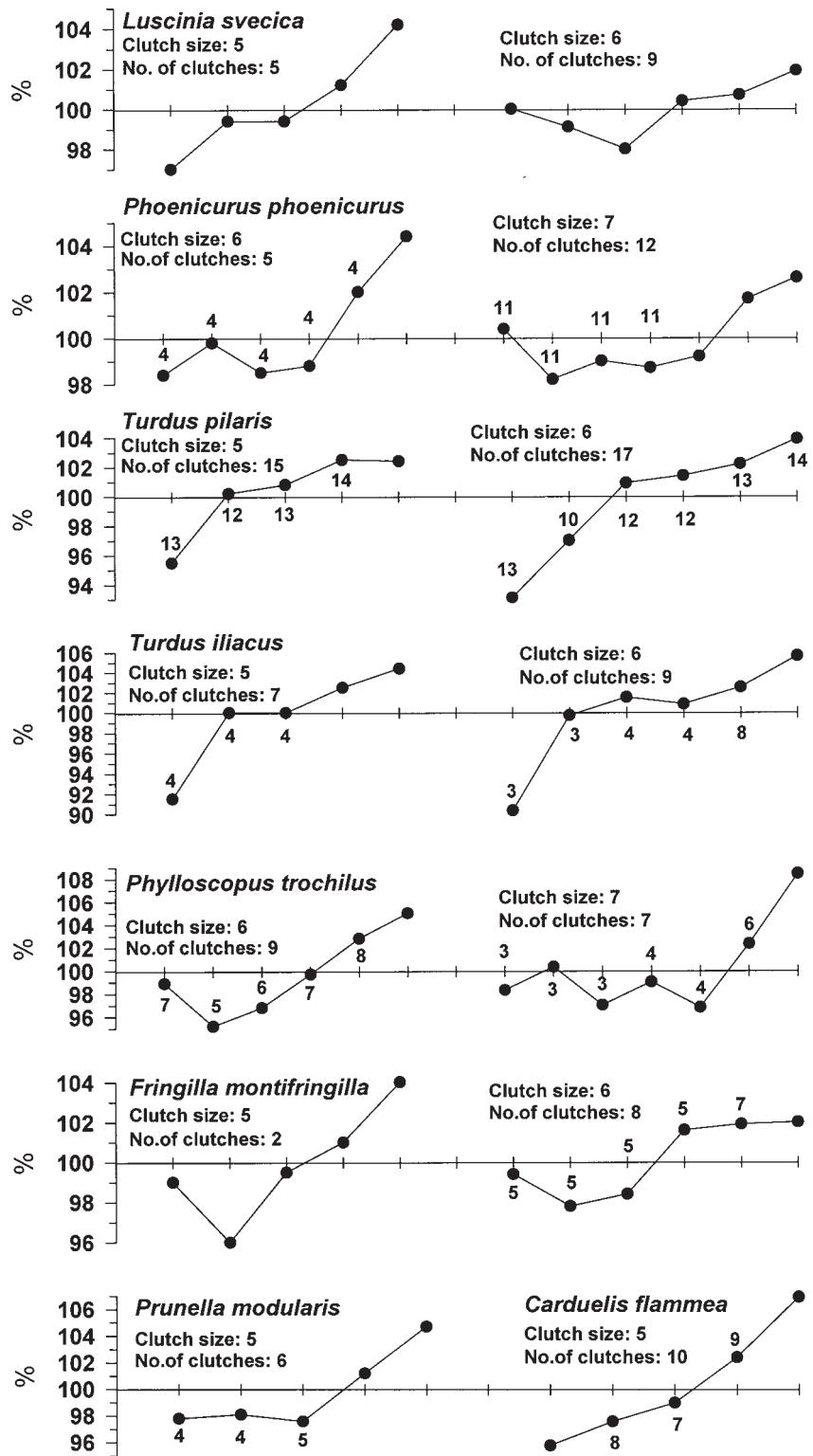


Figure 1. Diagrams showing the increase of the mean egg volume with the position in the laying sequence. Volumes are expressed as percentages of the clutch mean. The statistical analyses of the regression lines (not included in the diagrams) are found in Table 3. Number of eggs of each position is given only when not all clutches are included.

Diagram som visar hur äggstorleken (uttryckt i procent av medelstorleken i kullen) ökar i värpföljden. Säkerheten i denna ökning har prövats i Tabell 3. Antalet ägg står angivet när det är mindre än antalet tillgängliga kullar.

Table 4. The relative size (calculated volume) of the last laid egg as a percentage of the mean egg size of the clutch.

Relativa storleken (beräknad volym) av det sist värpta ägget i procent av äggens medelvolym i kullen.

Species Art	Clutch size Kullstorlek	Number of eggs Antal ägg	%
<i>Prunella modularis</i>	5–6	8	103.3±3.76
<i>Luscinia svecica</i>	5–6	14	102.6±2.57
<i>Phoenicurus phoenicurus</i>	6–7	18	103.3±3.38
<i>Turdus pilaris</i>	5–6	46	104.8±4.78
<i>Turdus philomelos</i>	5–6	16	103.1±3.95
<i>Turdus iliacus</i>	4–7	50	105.0±3.74
<i>Phylloscopus trochilus</i>	6–7	16	106.5±4.02
<i>Fringilla montifringilla</i>	5–7	13	102.1±4.43
<i>Carduelis flammea</i>	5–6	14	106.4±3.84

Dunnock *Prunella modularis*.

The average egg length and breadth seem to be somewhat shorter in Central Europe than in Lapland. This is supported also by the range values. The difference is about 0.3 to 1.1 mm and 0.1 to 0.6 mm for the length and breadth, respectively. The measurements given by Rosenius (1926) are also smaller than ours, possibly because Rosenius' collection comes largely from more southern parts of Sweden. The egg volume increases in the latter part of the laying sequence with the final egg about 3% larger than the mean of the clutch. Slagsvold et al. (1984) report a corresponding figure of 1.3 % for two Norwegian clutches.

Bluethroat *Luscinia svecica*.

The dimensions of 62 Swedish eggs (Rosenius 1926), 71 Norwegian eggs (Haftorn 1971), 59 eggs from Kilpisjärvi in northernmost Finland (about 69° N, 21° E) (Järvinen & Pryl 1980) and 21 eggs from "Lappland" (Makatsch 1976) are smaller than in this study. The mean of all eggs in the Finnish sample is 0.48 mm shorter in length and 0.28 mm in breadth than the eggs from Ammarnäs. These differences are probably not significant (see Discussion). A collection of 133 eggs from Sweden, of unknown local origin, are also small with a mean length of only 18.59 mm and breadth of 14.14 mm (Makatsch 1976, ref. to Jern & Rauer). The figures given by Schönwetter (1979) are of the same magnitude. Even smaller are 39 "lappländische Exemplare" with means of 18.23 mm (length) and 13.77 mm (breadth) (Rey 1912). The size appears to increase within the clutch from the first to the last egg, although significantly only in the 5-egg clutches

(Table 3). The ultimate egg exceeded the clutch mean by 2 – 3 % (5- and 6-egg clutches pooled) (Table 4).

Redstart *Phoenicurus phoenicurus*.

The breadth means of single eggs of large samples from England, Germany, Belgium, Czechoslovakia, Norway and Finland are all less than 14.0 mm, and so is the breadth reported by Rosenius (1926–1929) based on 78 eggs probably from southern Sweden. The mean breadth of 218 eggs from Central Europe is 14.13 mm (Makatsch 1976), i. e. the same as at Ammarnäs. The egg lengths give a bewildering picture. They conform with our sample in England, Germany and Czechoslovakia, are somewhat smaller in Belgium and Finland but larger in Norway (19.03 mm, n=36).

The regional variation of the egg size has previously been analysed by Ojanen et al. (1978). They conclude that eggs are shorter in Scandinavia than in Central Europe. The samples from Norway (36 eggs) and Swedish Lapland (66) deviate from this pattern. These samples are small compared to the Finnish one (200), so the conclusion of Ojanen et al. (1978) might still be correct. Järvinen (1991) calculated the mean egg volume of 94 clutches at Kilpisjärvi in northern Finland using a species specific formula derived by Ojanen et al. (1978). He reports a mean volume of $1.76 + 0.13 \text{ cm}^3$, which is less than the calculated volume, $1.81 + 0.15 \text{ cm}^3$, of the ten clutches in our study. This small difference, however, is not statistically significant ($t=1.014$).

Within clutches the size increased in the second half of the laying sequence (Table 1, Figure 1). The mean size of the final egg is 3.3% larger than the

clutch mean (Table 4). The corresponding values for Finnish Lapland were 1.8% in ten clutches with 5–8 eggs and 3.1% in four 7-egg clutches (Järvinen 1991). Ojanen et al. (1981), on the other hand, report a decrease of 0.2% in four clutches in central Finland. In some species the ultimate egg is smaller than the clutch mean (Slagsvold et al. 1984), but apparently this is not the case in the redstart.

Fieldfare *Turdus pilaris*

The egg measurements from Norway (Haftorn 1971) and Switzerland (Haas 1980) are approximately the same as at Ammarnäs. The lengths and breadths in Rosenius' collection from Sweden are 1.2 and 0.6 mm shorter, respectively. Thirteen clutches measured near Kristinehamn in southern Sweden ($59^{\circ} 20' N$, $14^{\circ} E$) agree with Rosenius' measurements, with a mean length of 28.8 ± 1.27 mm and breadth of 20.8 ± 0.69 mm (unpublished data). Both these samples are significantly smaller than the values in Table 1 ($t=2.705$, $p<0.01$ and $t=2.119$, $p<0.05$, respectively), while larger eggs are reported from Czechoslovakia (Hudec 1983). On the other hand, the mean egg length in Bayern, south Germany, is only 27.8 mm (Hohlt 1957). Apparently it is impossible to discern a consistent regional trend in egg size.

Mean egg volume of 64 Norwegian clutches is 6.79 ± 0.72 cm³ (Slagsvold 1982), similar to that in Table 2 ($t=0.793$). However, the egg volumes of the above-mentioned population in southern Sweden are significantly smaller (6.39 ± 0.66 cm³, $t=2.487$, $p<0.02$). The volume increases very clearly from the first to the last egg in the clutch (Table 3, Figure 1) with a relatively large last laid egg (Table 4). The latter is slightly larger than the last egg in 61 Norwegian clutches, $103.86 \pm 3.93\%$ (Slagsvold 1982), but the difference is not significant ($t=1.224$). The first laid eggs are remarkably small, their volumes being on average only $94.07 \pm 4.74\%$ ($n=30$) of the clutch mean.

The egg size seems to be rather stable over years at Ammarnäs since the clutch means did not differ between four investigated years (Table 4). Strictly, data from successive years will not be statistically independent because some females will return and breed again in the same area (cf. Nager & Zandt 1994). We do not consider this to be a problem since few of the ringed adult birds have returned to our study area (unpublished data).

The mean egg volumes did not differ significantly between the 5- and 6-egg clutches (6.87 ± 0.61 cm³, $n=22$, and 6.81 ± 0.51 cm³, $n=46$, $t=0.51$). Otto

(1979) found no difference in egg weights between the same clutch sizes in the Bergen area, western Norway.

Song Thrush *Turdus philomelos*.

The measurements from a number of Central European countries, England and Norway indicate that the eggs are long in Swedish Lapland, as all reported length figures from outside Lapland are less than 28 mm. The difference is about 1 mm. This tendency is not found in the breadth measurements. The lowest values are again found in Rosenius' Swedish collection (mean length of 79 eggs was 25.71 mm and breadth 19.96 mm). The position in the laying sequence was not determined for many enough eggs to give a reliable picture of the intraclutch variation. However, the mean volume of the last laid eggs is larger than the mean of the clutch (Table 4). Pikula (1971) found that the egg weights increased in the laying order in Czechoslovakia (last egg about 104% of the clutch mean (our calculation)). Therefore, it is probable that the pattern of the intraclutch variation is about the same as at Ammarnäs in Swedish Lapland.

Redwing *Turdus iliacus*.

The mean length and breadth of 78 Norwegian eggs (Haftorn 1971) as well as of seven clutches at Kristinehamn, southern Sweden (unpublished data), do not differ from those in Table 1. The eggs of Rosenius' collection are smaller with a mean length and breadth of only 25.63 mm and 18.26 mm, respectively. This is close to the 25.8 mm and 18.7 mm reported by Rey (1912) in 50 "lappländische Exemplare". The mean volume (Table 2) is the same as that of eleven 5- and 6-egg clutches in Norway (Slagsvold et al. 1984). The dimensions of the eggs do not vary much between seasons (Table 4) and only the changes in the mean length are significant.

The regression lines show that the average increase in egg size in the laying sequence are the highest among those presented in Table 3. The size of the last laid egg (Table 4) is similar to the 105.5% ($n=11$) of the clutch mean found by Slagsvold et al. (1984). The mean size of the first laid egg is surprisingly small ($90.3 \pm 0.87\%$ of the clutch mean), i.e. even smaller than that of *T. pilaris* (Figure 1).

Willow Warbler *Phylloscopus trochilus*.

In the Central European subspecies *trochilus*, the mean egg lengths are on average 1 to 0.5 mm shorter

than those of our northern *acredula*-population. An exception is the 15.8 mm mentioned by Schönwetter (1979) who also states that there occurs no significant racial variation. This conclusion is supported by the mean length of only 15.6 mm of 70 eggs of the Norwegian *acredula*-population (Haftorn 1971). On the other hand, Witherby et al. (1948) present an egg length of 16.1 mm (mean of 27 eggs) as characteristic of that subspecies. Within clutches, egg size increases in the laying sequence especially in last half (Table 3, Figure 1) with a very large final egg (Table 4).

Brambling *Fringilla montifringilla*.

The eggs at Ammarnäs seem to be 0.5 mm longer than 155 eggs from Norway and 665 eggs mentioned by Schönwetter (1979). The 256 eggs of Rosenius' collection are small with a mean of only 19.3 mm which is close to the values of 62 and 83 eggs from "Lappland" reported by Rey (1912) and Makatsch (1976), respectively. The egg breadth in Table 1 is only 0.1 to 0.3 mm larger compared to the collections referred to above. The size of the eggs increases in the laying sequence (Table 3, Figure 1).

Redpoll *Carduelis flammea*.

Our measurements do not differ much from those given by Rey (1912), Haftorn (1971) and Schönwetter (1984). Even Rosenius' collection presents mean values comparable with those at Ammarnäs but with a slightly larger length (16.8 mm, mean of 109 eggs). The Redpoll is in this respect unique among the nine species of this investigation. The intraclutch increase in egg size is evident from first to last egg (Table 3, Figure 1).

Discussion

The species survey above shows that eggs from Ammarnäs frequently are larger than those from Central Europe. This applies to both of the measured dimensions, although most often to length measurements. This relation is expected, as egg breadth varies less than length (e.g. Ojanen et al. 1978 with references). Most differences have not been possible to test statistically due to lack of information on clutch means. In some cases single egg means have been presented in the literature but these can not be used since eggs from one female are not independent samples. Furthermore, such pseudoreplication will inflate sample sizes and exaggerate the chance for

significant results. These shortcomings together with a general overview of the egg sizes of the different populations, referred to above, mean that it is not possible to discern any consistent regional trends.

The measurements presented by Rosenius (1926) are smaller than those at Ammarnäs. This could either depend on regional or local differences between populations within Sweden or differences in measuring technique. It is unlikely for several reasons that our technique with photos of transilluminated eggs would overestimate size. First, the sizes of the eggs of the three thrush species at Ammarnäs all exceed those of Rosenius' collection, and we measured these directly on fresh eggs in the field. Moreover, the photo measurements of the Redpoll eggs at Ammarnäs coincide with eggs of other samples including that of Rosenius. There is probably no reason, so far, to doubt that the tendency of the egg sizes at Ammarnäs to be larger than those of many other populations is real.

The large size of the eggs at Ammarnäs and the constancy of means between years (Table 5) might be explained by that the measurements at Ammarnäs were taken in a very productive habitat, productive meadow birch forest on a south-faced mountain slope. It is well known that a number of environmental factors, like food availability, affect egg sizes. For example, the biomass of lumbricids in the breeding area is positively correlated with egg size in the Fieldfare (Otto 1979). The access to food, such as insects and other invertebrates, often increases with the temperature, which is higher on the south-faced slopes compared to less sun-exposed surroundings.

Egg sizes in the laying sequence increased in all nine investigated species (Table 3). The increase was two to eight per cent from the smallest egg early in the sequence to the largest one, most often the ultimate or penultimate egg (Figure 1, Table 2). Eggs of small and large size could be found in most positions in the sequence, although most eggs in the latter half show a good agreement between laying and size orders. Several scientists have suggested that there is an adaptive value of this size difference in that it might decrease the effect of hatching asynchrony. Asynchronous hatching is still under intensive study (cf. reviews by Slagsvold & Lifjeld 1989, Magrath 1990, Stoleson & Beissinger 1995). Larger eggs are assumed to enhance the survival of the youngest chicks when hatching is asynchronous. Such hatching, as manifested by the preceding developmental asynchrony, is common among passerines in the Ammarnäs area (Enemar & Arheimer 1989).

Table 5. The egg dimensions (clutch means \pm SD) from different years of the *Turdus iliacus* and *T. pilaris* populations at Ammarnäs, Swedish Lapland. N = number of clutches.

Äggstorleken för rödvinge- och björktrastbestånden i Ammarnäs under olika år. N = antal källor.

Species Art	Year År	N	Length Längd mm	Breadth Bredd mm	Volume Volym cm ³
<i>Turdus iliacus</i>	1970	31	26.6 + 0.97	19.4 + 0.51	5.11 + 0.356
	1971	24	26.0 + 1.35	19.0 + 0.50	4.87 + 0.337
	1972	37	26.3 + 1.03	19.2 + 0.62	4.94 + 0.458
	1973	43	26.6 + 0.99	19.1 + 0.36	4.97 + 0.254
	1974	14	26.6 + 0.90	19.2 + 0.44	5.02 + 0.334
	1997	8	25.6 + 0.68	19.1 + 0.43	4.75 + 0.234
	ANOVA		p< 0.05	n.s.	n.s.
<i>Turdus pilaris</i>	1971	14	29.7 + 0.91	21.4 + 0.4	6.97 + 0.381
	1972	22	30.0 + 1.40	21.4 + 0.55	7.01 + 0.633
	1997	40	29.8 + 1.08	21.2 + 0.56	6.84 + 0.521
	1998	14	29.6 + 0.77	21.0 + 0.95	6.66 + 0.694
	ANOVA		n.s.	n.s.	n.s.

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References

- Bonnier, G. & Tedin, O. 1940. *Biologisk variationsanalys*. Bonniers, Stockholm.
- Cramp, S. 1988, 1992. *Handbook of the Birds of Europe, the Middle East and North Africa*. Vol. 5, 6. Oxford University Press, Oxford.
- Cramp, S. & Perrins, C. M. 1994. *Handbook of the Birds of Europe, the Middle East and North Africa*. Vol. 8. Oxford University Press, Oxford.
- Enemar, A. 1997. The egg size variation of the Treecreeper *Certhia familiaris* in southwestern Sweden. *Ornis Svecica* 7:107–120.
- Enemar, A. & Arheimer, O. 1989. Developmental asynchrony and onset of incubation among passerine birds in a mountain birch forest of Swedish Lapland. *Ornis Fennica* 66:32–40.
- Glutz von Blotzheim, U. N. & Bauer, K. M. 1985–1997. *Handbuch der Vögel Mitteleuropas*. Bd 10–14. AULA-Verlag, Wiesbaden.
- Haas, V. 1980. *Ethologische und ökologische Untersuchungen an süddeutschen Wacholderdrosseln unter besonderer Berücksichtigung des Koloniebrüters*. Diss. Fak. Biol. Univ. Tübingen.
- Hafstrom, S. 1971. *Norges Fugler*. Universitetsforlaget, Oslo.
- Hohlt, H. 1957. Studien an einer süddeutschen Population der Wacholderdrossel (*Turdus pilaris*). *J. Orn.* 98:71–118.
- Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77.
- Hudec, K. 1983. *Fauna CSSR, Ptaci-Aves*. Vol.3. Akademia, Praha.
- Järvinen, A. 1991. Proximate factors affecting egg volume in subarctic hole-nesting passerines. *Ornis Fennica* 68:99–104.
- Järvinen, A. & Pöylä, M. 1980. Nesting habits of the Bluethroat *Luscinia svecica* at Kilpisjärvi, Finnish Lapland. *Kilpisjärvi Notes* 4:1–7.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- Magrath, R. D. 1990. Hatching asynchrony in altricial birds. *Biol. Rev.* 65:587–622.
- Makatsch, W. 1976. *Die Eier der Vögel Europas*. Bd 2. J. Neumann-Neudamm, Berlin.
- Nager, R. G. & Zandt, H. S. 1994. Variation in egg size in Great Tits. *Ardea* 82:315–328.
- Ojanen, M., Orell, M. & Väistönen, R. A. 1978. Egg and clutch size in four passerine species in northern Finland. *Ornis Fennica* 55:60–68.
- Ojanen, M., Orell, M. & Väistönen, R. A. 1981. Egg size variation within passerine clutches: effects of ambient temperature and laying sequence. *Ornis Fennica* 58:93–108.
- Otto, C. 1979. Environmental factors affecting egg weight within and between colonies of Fieldfare *Turdus pilaris*. *Ornis Scand.* 10:111–116.
- Pikula, J. 1971. Die Variabilität der Eier der Population *Turdus philomelos*, Brehm 1831, in der CSSR. *Zool. Listy* 20:69–83.
- Rey, E. 1912. *Die Eier der Vögel Mitteleuropas*. Verlag von Fr. Krüger.
- Rosenius, P. 1926–1949. *Sveriges Fåglar och Fågelbon*. CWK Gleerup, Lund.

- Schönwetter, M. 1979 & 1984. *Handbuch der Oologie*. Bd 2 & 3. Akademie-Verlag, Berlin.
- Slagsvold, T. 1982. Clutch size, nest size, and hatching asynchrony in birds: experiments with the Fieldfare (*Turdus pilaris*). *Ecology* 63:1389–1399.
- Slagsvold, T. & Lifjeld, J. T. 1989. Constraints on hatching asynchrony and egg sizes in the Pied Flycatchers. *J. Anim. Ecol.* 58: 837–49.
- Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, Ö. & Husby, M. 1984. On the adaptive value of intraclutch eggsizes variation in birds. *Auk* 101:685–697.
- Stoleson, S. H. & Beissinger, S. R. 1995. Hatching asynchrony and the onset of incubation in birds, revisited. When is the critical period? *Current Ornithology* 12:191–270.
- Svensson, B. W. 1978. Clutch dimensions and aspects of the breeding strategy of the Chaffinch *Fringilla coelebs* in northern Europe: a study based on egg collections. *Ornis Scand.* 9:66–83.
- Verheyen, R. 1967. *Oologia Belgica*. Bruxelles.
- Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. 1948. *The Handbook of British Birds*. H. F. & G. Witherby Ltd, London.
- på medelvärdet för varje kulls medelvärde. Anledningen är att det första medelvärdet återfinns i de stora handböckerna, medan det andra är det som kan användas statistiskt vid jämförelse mellan olika regioners äggstorlekar. Med hjälp av längd- och breddmåtten har äggens volym beräknats, eftersom denna tar samtidig hänsyn till de båda äggmåtten, vilket är en fördel vid vissa jämförelser. De beräknade volymernas medelvärden för de nio arterna presenteras i Tabell 2. I Figur 1 visas hur äggvolymen ändras inom en kull beroende på äggets position i värföljden. Som regel gäller att volymen successivt ökar, i varje fall i den senare delen av värtiden. Ökningen från första till sista ägg har prövats statistiskt och befunnits vara säker i samtliga fall utom ett (Tabell 3). I de flesta fallen är det näst sista eller sista ägget störst. Sista äggets storlek i procent av äggens medelvolym i kullen redovisas i Tabell 4.
- Kullar av rödvingetrast och björktrast har mätts under flera år. En jämförelse mellan medelvärdena för de olika åren visar att äggstorleken håller sig förvånande konstant (Tabell 5). Den enda någorlunda säkra avvikelsen utgörs av de relativt korta äggen hos rödvingetrast 1997. Dock var antalet mätta kullar det året litet och resultatet därmed mindre tillförlitligt.

Sammanfattning

Äggstorleken hos nio tättingarter i fjällbjörkskog i södra Lappland

Inledning och metod

Under fågelstudierna i Ammarnäs-området i södra Lappland (LUVRE-projektet) har längd och bredd för åtskilliga fågelägg mätts, dels med skjutmått i samband med bofynd i terrängen, vilket gäller trastarna, dels på fotografier av genomlysta äggkullar av övriga mindre arter. Dessa data har till största delen insamlats under lång tid (1971–1998) som biprodukt av undersökningar, som gällt andra problem än dem som har med äggstorlekarna att göra. I vissa kullar har äggen numrerats i den ordning de värvs. Detta har skett i samband med dagliga besök under värtiden. Ett användbart material har erhållits för nio arter, nämligen järnsparr, blåhake, rödstjärt, björktrast, taltrast, rödvingetrast, lövsångare, bergfink och gråsiska. Praktiskt taget alla bofynd har gjorts i den rika fjällbjörkskogen på sydslutningarna av fjället Gaisatjäkke och Valle.

Resultat

Resultaten redovisas i ett antal tabeller och en figur. Grundmaterialet sammanfattas i Tabell 1, där antalet ägg och kullar för de olika arterna redovisas tillsammans med två medelvärdena av äggmåtten (med spridningsmått, SD) för varje art, det ena uträknat direkt på totalantalet mätta ägg, det andra

Jämförelser

Hur stora är äggen i Ammarnäs jämfört med äggen av samma arter på andra håll? Det finns ett rikt material att jämföra med, vilket dock är av begränsad användbarhet. De sentida stora handböckernas uppgifter har som regel hämtats från framförallt äldre men även några yngre sammanfattande verk, som helt ägnas åt fågeläggens utseende och mått. Dessa handböcker i oologi är produkter av forna tiders äggsamlande. Man får där medelvärden på äggens längd och bredd men nästan aldrig några statistiskt användbara spridningsvärden. Variationen karakteriseras istället i form av de funna maxi- och minimimåtten. Därför kan som regel hållbarheten i skillnaderna mellan äggstorlekarna på olika håll inte prövas. Därtill kommer att det ofta brister i uppgifterna om de studerade äggens ursprung. Därför stannar det jämförande arbetet här vid konstaterade antydningar eller tendenser, vilka må bekräftas eller förkastas i en framtid, då ett användbart datamaterial finns att tillgå.

För både järnsparr och blåhake visar äggen i Ammarnäs något högre medelvärden på längd och bredd än på andra håll i nord- och mellaneuropa. För den hålbyggande rödstjärten finns särskilt rika möj-

ligheter till jämförelser. Äggen är som regel smalare på andra håll i Europa medan ägglängden kan visa både högre och lägre värden beroende på ursprung. I nordligaste Finland är äggvolymen något mindre än i Ammarnäs. I detta fall kunde skillnaden testas statistiskt, vilket visade att den inte är signifikant.

Av trastarna upptäcktes björktrast och taltrast lika stora eller större ägg än på andra håll. Alla uppgifter om taltrastens ägglängd understiger 28 mm, medan Ammarnäs-äggens medellängd visade sig vara inte mindre än 28,5 mm. För den nordliga arten rödvingetrast gäller samma äggstorlek i Norge som i Ammarnäs. Den ene av oss (O.A.) mätte våren 1971 ett antal kullar av björktrast och rödvingetrast i närheten av Kristinehamn. Björktrastäggen var 1 mm kortare och 0,4 mm smalare där än i Ammarnäs, en statistiskt säker skillnad. Rödvingeäggen visade däremot god överensstämmelse mellan de båda lokalerna.

För lövsångarens del är äggen 1 till 0,5 mm kortare i de mellaneuropeiska bestånden, som ju tillhör en annan ras, *trochilus*, än den i Ammarnäs, *acredula*. Sistnämnda ras finns också i Norge, men även där är äggen mindre än i Ammarnäs, tyvärr. Äggstorleksförhållande till rastillhörigheten är värd en egen undersökning.

Av de två återstående arterna upptäcktes bergfinken i Ammarnäs större äggmått än vad fallet är i Norge eller i andra äggssamlingar med påstått lappländskt ursprung. Gråsiskan, slutligen, är unik i det att alla uppgifter om äggstorleken i stort stämmer med måttet i Ammarnäs.

Diskussion

Av jämförelsen ovan framgår klart, att äggen av nästan alla de studerade nio arterna i Ammarnäs tenderar att vara lika stora eller större än äggen av samma arter på annat håll, främst i Mellaneuropa. Det gäller framförallt längdmåtten, vilket inte förvånar, eftersom det är känt sedan länge, att äggens längd varierar mer än bredden. Skillnaderna är inte

stora. Det rör sig om någon enstaka mm eller del därav. Man får räkna med att en icke så liten del av de konstaterade skillnaderna är en följd av slumpens verk.

En egendomlighet är det faktum att de äggmått, som publicerats av ornitologen och äggsamlaren Paul Rosenius i hans magnifika flerbandsverk "Sveriges Fåglar och Fågelbon", så genomsättande har lägre värden, dock med undantag för gråsiskan för vilken måtten stämmer med dem från Ammarnäs. Man kan fråga sig, om skillnaden beror på olikheter i tekniken att mäta (på foton av äggen i vårt fall, direkt på (de urblåsta?) äggen i Rosenius' fall). Det förefaller dock inte sannolikt, eftersom även trastäggen i Ammarnäs var störst, trots att måtten på dessa togs direkt på äggen i fält.

Det bör understrykas att de studerade äggen i Ammarnäs nästan uteslutande härstammar från häckningar i en gynnsam miljö, den produktiva ängs- och björkskogen. Det innebär rik näringstillgång, gynnat av den goda solvärmens på den aktuella sydslutningen. Det är känt att såväl näringstillgång som omgivningstemperatur positivt påverkar äggstorleken. Det är möjligt att de äggssamlingsplatser, som ligger till grund för de mindre äggmåttet i andra regioner, innehåller en större andel från häckningar i fattiga miljöer. Äggstorleken kan också påverkas mer eller mindre av flera andra faktorer, vilka dock lämnas därhän i detta sammanhang.

Genomsnittligt förmår fågelhonorna i Ammarnäs att öka äggstorleken under värpningens gång, i synnerhet under dennes senare del. Detta är en vanligt förekommande egenskap hos tättingar, ofta kombinerad med att ruvningen påbörjas innan äggkulpen är färdigvärpt. Detta innebär att de sist lagda äggen kläcks upp till mellan ett och två dygn senare än de övriga. Eftersom de sista, större äggen ger upphov till lite tyngre ungar, anses dessa därmed ha ökade möjligheter att klara sig i konkurrensen med de tidigare kläckta syskonen, som ju hunnit växa till sig en smula innan kullen är färdigkläckt.